

INVESTMENT IN NEST DEFENSE BY NORTHERN FLICKERS: EFFECTS OF AGE AND SEX

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ABSTRACT.—At early breeding stages, male woodpeckers invest heavily in nest construction and defense, but parental contributions to brood defense among Picidae are not well known. We studied the Northern Flicker (*Colaptes auratus*) to determine whether sex, age, brood size, body size, or body condition influenced defense behavior. When presented with a model predator (red squirrel, *Tamiasciurus hudsonicus*) during the brood-rearing period, parents exhibited a range of behaviors, such as blocking the nest hole, diving at the model, and striking the model; however, defense scores did not differ between males and females aged 1, 2, or 3+ years old. Although we predicted that defense level would be positively correlated with brood size, we found no such relationship. Adult body size and condition also were not related to defense intensity. We conclude that the sexes may exhibit similar levels of defense because they have similar apparent annual survival rates and males are only slightly larger than females. If flickers optimize clutch size according to the number of offspring they can rear, then there may be no relationship between defense and brood size. Received 20 September 2005, accepted 6 July 2006.

Although nest defense may deter predators, it may place the parent bird at considerable risk while requiring significant energy expenditure (Blancher and Roberstson 1982, Nealen and Breitwisch 1997, Olendorf and Robinson 2000). For many birds, the intensity of nest defense may increase (1) as the breeding season and reproductive value of the brood increases (see Montgomerie and Weatherhead 1988 for a review), (2) as the potential for renesting declines (Andersson et al. 1980), and (3) with clutch or brood size (Olendorf and Robinson 2000). Moreover, the intensity of defense may depend on the sex of the parent defending the nest (Breitwisch 1988, Sproat and Ritchison 1993, Nealen and Breitwisch 1997).

Age may be correlated with the level of nest defense for several reasons, but this has rarely been tested (Veen et al. 2000). Older birds have a lower probability of future reproduction; thus, they should invest more in broods than younger individuals (Hatch 1997). In addition, it is often difficult to separate the effects of age from experience with predators because they are often directly correlated. Similar to older birds, birds with more

experience also may be willing to defend their nests more aggressively (Veen et al. 2000).

Levels of defense also may vary between the sexes (e.g., Breitwisch 1988, Sproat and Ritchison 1993, Tryjanowski and Golawski 2004) because of intersexual differences in future survival and body size (Montgomerie and Weatherhead 1988). The sex with the lower survival rate and, consequently, the lower probability of future breeding, should defend broods more vigorously than its partner (Montgomerie and Weatherhead 1988). Mortality is usually female biased in many bird species, likely as a result of high reproductive costs (Promislow et al. 1992). Generally, the larger sex defends the nest more aggressively, perhaps because the risk of injury is lower or because larger birds are able to mount strong attacks (Tryjanowski and Golawski 2004). Because healthy birds may have relatively greater energy reserves, they may take more risks when defending their nests than birds in poorer condition (Martin and Horn 1993). For example, females may be in poorer condition after incubation and defend the nest less aggressively than the male (Sproat and Ritchison 1993).

Cavity nesters may rely more on the inaccessible or cryptic nature of their nest than on active nest defense (Weidinger 2002); however, there have been few studies of woodpecker behavioral responses to predators at the nest site. Wiebe (2004) examined responses of the Northern Flicker (*Colaptes auratus*)

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to the European Starling (*Sturnus vulgaris*)—a kleptoparasite of cavity nests (Kappes 1997)—but found no sex- or age-related differences in cavity defense. Ingold (1994) also described aggressive interactions between starlings and flickers, but did not examine sex or age differences in these behaviors. Lawrence (1967) described woodpeckers defending their nests from inside their cavities, engaging in alarm vocalizations and diving attacks; she also reported a male Northern Flicker that delivered a blow with its beak to a squirrel entering a nest hole, effectively deterring the squirrel from entering.

In this study, we presented a model predator (red squirrel, *Tamiasciurus hudsonicus*) at nest sites of Northern Flickers to examine adult nest-defense behavior in relation to age, sex, brood size, body size, and body condition. Because flickers are relatively short-lived and their probability of survival is independent of age (Fisher and Wiebe 2006a), we predicted that there would be no differences in defense between young and older birds. Similarly, mark-recapture models suggest only a 2% difference in annual survival rate between the sexes (Fisher and Wiebe 2006a), and the sexes invest about equally in nestling provisioning (Moore 1995, Wiebe and Elchuk 2003). Thus, we predicted that male and female flickers would defend their broods with similar intensity. We also predicted that individuals in better condition and with larger broods would defend their nests more aggressively.

METHODS

Study site and study species.—Our study site was near Riske Creek, British Columbia (51° 52' N, 122° 21' W), and encompassed approximately 100 km²; 90–120 pairs of flickers nest there each year (Fisher and Wiebe 2006a). Habitats on the site are patchy and variable. Flickers prefer grasslands for foraging (Elchuk and Wiebe 2003) and patches of quaking aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) for nesting (Martin and Eadie 1999). Continuous forests of Douglas-fir (*Pseudotsuga menziesii*) and hybrid spruce (*Picea engelmannii* × *P. glauca*) also occur.

Flickers migrate to the area in mid-April and begin egg-laying in early- to mid-May

(mean clutch-initiation date = 13 May, range = 26 April–2 July; Moore 1995, K LW unpubl. data). Each year since 1998, the area has been surveyed in spring (22 April–15 May, 1998–2005) for finding newly excavated cavities and to check old cavities for new breeding pairs (flickers tend to reuse old cavities more often than other woodpeckers; Moore 1995, Aitken et al. 2002, Wiebe et al. 2006). Tape-recorded territorial playback calls also were used to locate flicker territories and nest sites. Average clutch size in this area is eight eggs and mean number of young fledged per successful nest is six (Wiebe 2003). Once a clutch was complete, we cut a small door into the side of the nest tree for access to adults, eggs, and nestlings (see Wiebe 2001). Flickers seem to tolerate the doors and readily re-use such cavities (Fisher and Wiebe 2006a). Approximately 18% of monitored nests are depredated annually by mammalian predators, mainly red squirrels (Fisher and Wiebe 2006b).

We captured flickers by flushing individuals from the nest cavity into a small net placed over the cavity entrance (Fisher and Wiebe 2006b). Three colored plastic and one aluminum band were attached to each individual to aid in individual identification (>95% of the known annual breeding population is color banded and individually identifiable). During banding, we used molt criteria to determine the birds' ages (up to 4 years old; Pyle et al. 1997). We developed an index of flicker body size (i.e., score on the first axis of a principle components analysis based on six measures: bill depth, and lengths of the wing, bill, tail, tarsus, and ninth primary) and body condition (i.e., residuals of a regression of body mass on body size); because of sexual size dimorphism, we made separate calculations for males and females (see Wiebe and Swift 2001). A year-specific estimate of body condition was made only for individuals that were trapped and weighed in 2003 and 2004; thus, only individuals captured during 2003 or 2004 were included in analyses with body condition as a covariate (see below). We assumed that body size (i.e., the structural size of an individual and not body mass) did not change from year to year.

Model presentations.—Birds with altricial young generally defend their nests most

strongly during the nestling stage and as nestlings age (Montgomerie and Weatherhead 1988). We measured nest defense when nestlings were 10–15 days old to control for effects of nest stage and nestling age on defense behavior. At each nest, we tested nest defense once with a predator (taxidermic model of a red squirrel) and once with a control (taxidermic model of a Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*, or a Cedar Waxwing, *Bombycilla cedrorum*). The same individuals were tested only once with each model during the 2-year study to avoid potential habituation of parents to the models (Knight and Temple 1986a, 1986c). Blackbird and waxwing models were used as controls because they are both common in the study area and neither poses a threat to flicker broods (Wiebe 2004). In 2004, during 60% of control trials we used the waxwing because the blackbird model was irreparably damaged from transportation to and from trials.

Predator and control trials were conducted randomly at a given nest, with 1–5 days between trials (i.e., one trial = one model presentation). Because the perceived threat from a predator could vary with distance between the predator and the nest (Rätti 2000), we fastened the models at a fixed distance (1 m below the cavity entrance) with a bungee cord tied to the tree trunk. The model squirrel was attached to a small, flat board base that was then attached to the tree trunk. Control models were mounted in an upright, perched position on a natural branch, which was then attached to the tree trunk. During a given trial, territorial “chatter” calls of squirrels or songs of Yellow-headed Blackbirds or Cedar Waxwings were played at the base of the nest tree to increase model detectability (Ghalambor and Martin 2002). After models were placed at the nest, we retreated to a concealed position ≥ 15 m away to record responses of the returning parents.

The first variable we recorded was response time of the adult (i.e., sec between when we had set up the model and were hidden, to when the parent returned and we judged it was within 10 m of the nest and in sight of the model). Ten meters from the nest was usually the maximum distance from which we could observe a bird responding, because of dense foliage around some nests. We were confident

that the flicker was responding to the model at distances ≤ 10 m from the nest once we judged that it could see the model. If parents did not return to within 10 m and in sight of the model in 1 hr, then these trials were removed from all analyses. After an adult(s) returned within ≤ 10 m, we recorded its behavior for 5 min (if both parents returned simultaneously, we treated them as individual responses). Flickers respond to models with slow, deliberate movements (Wiebe 2004), so the 5-min period should have provided a representative sample of behavior. We quantified defense levels based on four behaviors recorded during the 5-min period: (1) number of alarm calls (*peah* and *wicka* calls; Moore 1995); (2) the closest distance that the responding parent approached the model (m; a visual estimate); (3) whether or not the parent dived at or hit the model (dichotomous variable); and (4) time (sec) an individual spent inside the cavity during each trial (flickers entered cavities and then peered back out, usually with their beaks protruding from the cavity entrances). Time spent in the cavity should reflect investment in nest defense because blocking the entrance prevents predation of the nest (Cordero and Senar 1990). Assessing the risk a parent incurs by blocking the cavity entrance is difficult. This defensive strategy may be safer than others because most of the parent's body is inside the cavity (Cordero and Senar 1990); conversely, there are no avenues of escape for the parent.

Statistical analyses.—Response time was square-root transformed to meet assumptions of normality, and we analyzed it separately from other defense variables because it was unlikely to have been influenced by model type (parents presumably had not had time to see the model before returning). We used an ANCOVA to test whether age, sex, brood size, and/or body condition affected response time to the predator model (we assumed that the structural size of an individual would not influence response time). Because data transformations of the other four defense variables did not result in normality, we used non-parametric tests for subsequent analyses. Statistical significance was set at $P < 0.05$.

With respect to the four nest-defense variables, there was no difference between control model types (blackbird versus waxwing;

Mann-Whitney *U* and Fisher Exact tests: all $P > 0.47$). Similar tests also showed that there were no significant differences between years in terms of responses to control and predator models (all $P > 0.12$). Therefore, we pooled all responses (for years and control models) in subsequent analyses.

We first analyzed each defense variable singly to determine which differed significantly between control and squirrel models, without any other effects. This allowed us to eliminate model type as a variable if it was non-significant, thus simplifying subsequent models involving age class, sex, brood size, body size, and body condition. We used paired tests (Wilcoxon's signed-rank tests) to analyze minimum distance to the model, time in the cavity, and number of alarm calls to account for both predator and control trials taking place at the same nest. This approach may have been more stringent than necessary because it was not necessarily the same individual that responded to each trial; however, independent test results were consistent with those of the paired tests. We used a Fisher's exact test to compare the frequency of diving at the squirrel versus the control models. All means presented are \pm SD.

After separate analysis of each defense behavior (see results), we constructed an overall defense score based on the three variables that differed significantly between control and predator models. This score was used in subsequent analyses involving the relationship between various parental attributes and strength of response to the squirrel model. A score of 1 indicated the bird returned to the nest and was judged to be within sight of the model but did not dive at the model or enter the cavity, and always remained ≥ 2 m away from the model (there is a low probability that a squirrel could contact the parent at a distance of 2 m). A score of 2 indicates that the parent approached ≤ 1 m from the predator model but otherwise performed no other nest-defense behaviors. In developing score 2, we assumed that a squirrel might be able to physically contact a flicker ≤ 1 m away and that parents approaching within 1 m were placing themselves at a greater risk than those in score category 1. Responses in category 2 included perching on the cavity lip from the outside or on a branch within 1 m of the model. A score

TABLE 1. Sample sizes of Northern Flickers responding to a model predator (red squirrel) or control (Yellow-headed Blackbird or Cedar Waxwing) placed at their nests during the brood-rearing stage at Riske Creek, British Columbia (2003 and 2004 data pooled). Totals include instances in which both parents responded to the models, plus those in which only one parent responded; thus, sample sizes are larger than the total number of trials conducted for each model type.

Model type (total no. trials)	Sex	Age	<i>n</i>
Control (91)	Male	1 year	15
		2 years	17
		3+ years	25
	Female	1 year	19
		2 years	16
		3+ years	15
Predator (94)	Male	1 year	17
		2 years	19
		3+ years	24
	Female	1 year	20
		2 years	14
		3+ years	13

of 3 indicates that the parent entered the cavity and blocked it from the inside. Finally, a score of 4 indicates that birds dived at or hit the model, indicating the riskiest and most energetically expensive behavior to a defending adult.

For statistical analyses involving age, we categorized males or females as either 1, 2, or 3+ years old, such that there was at least a sample size of 13 in each age category (Table 1). A further subdivision of age was not possible to analyze statistically, as it would have resulted in some categories with a sample size < 5 . We used a Kruskal-Wallis test to examine whether the median defense scores of birds in the six different age-sex classes differed. To analyze the effect of brood size on defense score (a categorical variable), we used Spearman's rank correlations. Body size and condition met assumptions of normality; therefore, we could use parametric tests (two-factor ANOVA) to assess the relationship between defense score and sex on body size and condition (dependent variables).

RESULTS

We conducted 91 control trials and 94 predator trials at 94 Northern Flicker nests in 2003 and 2004. Control trials were not conducted at three nests because nestlings were > 15 days old by the time the second model could

TABLE 2. Effects of sex, age class (1, 2, and 3+ years old), brood size, and body condition of flicker parents on their response time (see description in text) to a model nest predator presented at the nest during the brood-rearing stage at Riske Creek, British Columbia, 2003 and 2004. No predictor was significant according to a 2-factor ANCOVA ($n = 84$ individuals) using Type III sums of squares.

Effect	SS	df	F	P
Sex	231.67	1	1.18	0.29
Age	181.15	2	0.44	0.65
Sex \times age	438.81	2	1.06	0.35
Brood size	16.50	1	0.56	0.46
Body condition	589.02	1	2.84	0.10
Sex \times brood size	211.50	1	1.02	0.32
Age \times brood size	92.43	2	0.22	0.80

be presented. Parents occasionally returned together to defend the nest (16 out of 91 control and 13 out of 94 predator trials) and responses by these individuals were considered to be independent trials (i.e., two parents responding increased sample size by two). Sample sizes of responding parents of both age classes and sexes varied according to model type (Table 1).

Response time and defense behaviors.—The mean overall response time to the predator model was $1,090 \pm 876$ sec ($n = 107$). There was a weak trend ($P = 0.10$) that birds in better condition responded to the predator model more quickly, but there was no effect of age, sex, brood size, or body condition, and there were no interactions (Table 2).

Flickers dived significantly more at the predator model (26% of trials) than at the control (2% of trials; Fisher’s exact test: $P < 0.001$). Parents also approached the predator model more closely ($3 \text{ m} \pm 4$) than the control model ($5 \text{ m} \pm 4$; Wilcoxon’s signed-rank test: $Z = -4.98$, $P < 0.001$). During the 5-min trials, flickers spent significantly more time in their cavities when responding to the predator model than to the control model ($16\% \pm 33$ versus $5\% \pm 20$, respectively; Wilcoxon’s signed-rank test: $Z = -2.35$, $P < 0.001$). Parents gave *wicka* and *peah* alarm calls in 36% of the trials, but there was no effect of model type on the number of alarm calls (mean number of alarm calls = 11 ± 32 and 18 ± 37 in response to predator and control models, re-

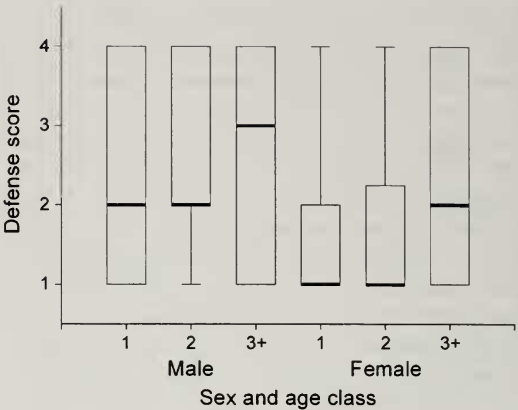


FIG. 1. Nest-defense scores of parent flickers did not differ by sex and age categories when responding to a model predator (red squirrel) placed at their nest during the brood-rearing stage in Riske Creek, British Columbia, 2003 and 2004. Bold horizontal lines represent median defense scores, boxes represent 25th and 75th percentiles, and error bars represent 10th and 90th percentiles. Because several birds within each age and sex category received the same defense score, some 10th, 25th, 75th, and 90th percentiles overlap; thus, symbols for each age and sex class are not necessarily apparent.

spectively; Wilcoxon’s signed-rank test: $Z = -1.41$, $P = 0.16$).

Traits of the parent and brood.—The median defense score for males ≥ 3 years of age was marginally higher than of any other age-sex category (Kruskal-Wallis test: $\chi^2 = 6.63$, $df = 3$, $P = 0.085$; Fig. 1). Brood sizes of parents tested with the squirrel model ranged from 2 to 9, but there were no significant correlations between brood size and nest-defense score for the six age-sex classes when considered separately (Spearman’s rank correlations: all $P > 0.28$, but two-year old males showed a marginally significant trend of defending smaller broods more aggressively, $r = -0.45$, $P = 0.060$). Similarly, with all ages and sexes combined, there was no effect of brood size on defense score (Spearman’s rank correlation: $r = 0.02$, $P = 0.83$). In another analysis, we categorized brood sizes as small (≤ 6 chicks, $n = 45$) versus large (≥ 7 chicks, $n = 62$). Approximately 30% of individuals with large broods exhibited the most intense defensive behavior (score = 4), whereas 22% of individuals with small broods had score 4; however, the overall frequency of

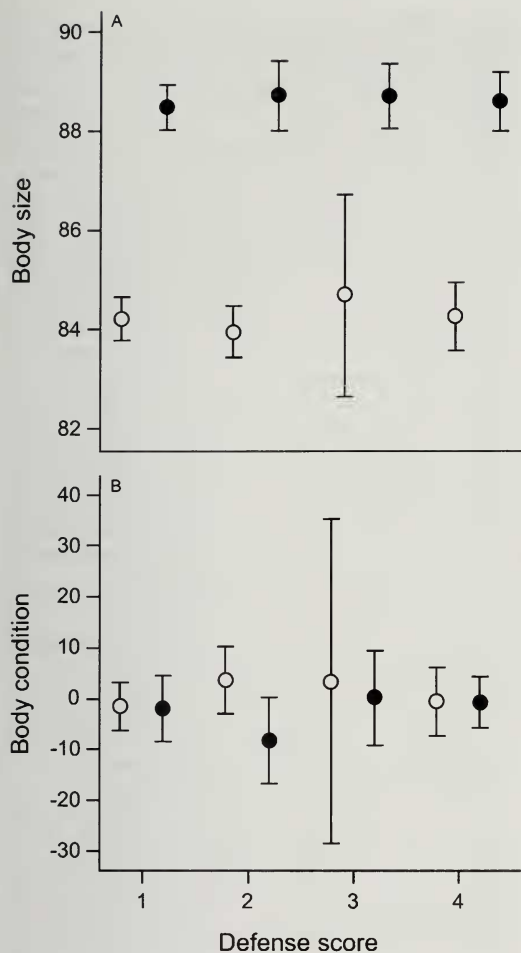


FIG. 2. Mean and 95% CI of (A) body size and (B) body condition for male (filled circles) and female (open circles) Northern Flickers performing four levels of nest defense (1 = least, 4 = greatest; see text for description of defense scores) in response to a model predator placed at nests during the brood-rearing stage at Riske Creek, British Columbia, 2003 and 2004. Body size differed between the sexes, but defense scores did not vary with body size or condition.

defense scores was not associated with brood size ($\chi^2 = 2.48$, $df = 3$, $P = 0.48$).

As expected, adult body size was significantly associated with sex (males were structurally larger than females; two-factor ANOVA: $F = 345.67$, $df = 1$, $P < 0.001$), but there was no relationship between body size and defense score ($F = 0.33$, $df = 3$, $P = 0.80$; Fig. 2), nor was there a sex \times defense score interaction ($F = 0.41$, $df = 3$, $P = 0.75$). Similarly, there was no relationship between body con-

dition and defense score (two-factor ANOVA: $F = 1.48$, $df = 3$, $P = 0.84$) for either sex ($F = 2.13$, $df = 1$, $P = 0.15$; Fig. 2) or a sex \times defense score interaction ($F = 1.48$, $df = 3$, $P = 0.23$; Fig. 2).

DISCUSSION

Relationship between sex and nest defense.—Although a model predator may not elicit the same intensity of nest defense as a real predator, the fact that flickers responded to it more intensely than to the control model suggests that they did perceive danger. Consistent with initial predictions, we found no differences between nest defense of male and female flickers. Although many studies have revealed sex-related differences in nest defense among birds (Gill and Sealy 1996, Cawthorn et al. 1998, Pavel and Bureš 2001, Griggio et al. 2003), others have not, including studies on the American Goldfinch (*Carduelis tristis*; Knight and Temple 1986b) and Red-backed Shrike (*Lanius collurio*; Tryjanowski and Golawski 2004). Adult male and female American Goldfinches may exhibit equal defense responses because they are monogamous and both sexes are required to raise the young (Knight and Temple 1986b). Tryjanowski and Golawski (2004) suggested that net costs and benefits of nest defense by male and female Red-backed Shrikes were equal because males were larger than females, but females had greater confidence of parenthood. For flickers, the sex-related differences in survival (male survival is 2% lower than that of females; Fisher and Wiebe 2006b), body size (males are ~3% larger than females; Moore 1995, Wiebe 2000), and investment in the current brood (Moore 1995, Wiebe and Elchuk 2003) are likely too small to alter the costs and benefits of sex-related nest defense. Among cavity nesters, male Eastern Screech-owls (*Otus* [currently *Megascops*] *asio*) defend nestlings more aggressively than females (Sproat and Ritchison 1993), as do male Great Tits (*Parus major*; Currio and Onnebrink 1995) and male Tree Swallows (*Tachycineta bicolor*; Winkler 1992).

Age and nest defense.—In general, we found no significant association between age and nest defense, although males ≥ 3 years old tended to engage in more risky defense behavior (attributed to their greater tendency to

block the cavity entrance) than the other groups. Blocking the cavity entrance may be used by cavity nesters to prevent usurpation of cavities (Cordero and Senar 1990). With the head and bill in striking position at the entrance hole, it also may be an effective strategy for fending off an attack while minimizing risk to the rest of the parent's body. The lack of strong age or sex effects on any defense behavior suggests that individuals of different ages perceive the overall costs and benefits of nest defense in a similar way.

According to economic models of nest defense (Montgomerie and Weatherhead 1988), an older bird should defend its current brood more aggressively than a younger bird because it has a lower future reproductive potential; however, we found no evidence for this in flickers. Winkler (1992) explained that age-independent survival probabilities precluded an effect of age on nest defense by Tree Swallows. Similarly, the annual apparent survival rates (42%) for flickers do not vary with age, and the birds are relatively short-lived (Fisher and Wiebe 2006b), so it is probably not surprising that age has little influence on defense intensity.

Although future reproductive potential is one component that could lead to age-dependent nest defense, experience also may be a key factor if defense is learned and becomes less risky for the adult over time (Montgomerie and Weatherhead 1988). We could not separate age from experience in our study and it is impossible to know the previous experience that a wild bird may have had with a predator.

Effects of body size and condition on nest defense.—It was surprising that neither body size nor condition were positively associated with our measures of flicker nest defense. Although sexual-size dimorphism is often cited as contributing to differences in nest defense between the sexes (Tryjanowski and Golawski 2004), effects of body-size differences within the sexes have rarely been tested (Hamer and Furness 1993, Radford and Blakey 2000). If large and small birds are both effective nest defenders for different reasons—for example, if small individuals have greater maneuverability and large individuals are more powerful—then overall costs and benefits may be similar for each (Montgomerie and Weather-

head 1988). The few studies that have tested for within-sex effects of body condition have been equivocal at best, ranging from no effect (Radford and Blakey 2000) to a sex-specific effect (Winkler 1992, Hamer and Furness 1993). There is little direct evidence that body condition affects the intensity of active defense in any species, but good nutrient reserves may allow a parent to reduce foraging time away from the nest and be more attentive to the nest site during incubation and brooding (Slagsvold and Lifjeld 1989, Wiebe and Martin 1997); in turn, these factors would result in greater nesting success (Chastel et al. 1995). We found some evidence that birds in better body condition responded more quickly to the predator model, which may provide support for this hypothesis. Flicker condition was measured in the late stages of incubation or early stages of brooding when parents could be captured; thus, they may not have been in exactly the same condition at the time of our defense trials (about 10–15 days later). However, if relative rankings of body condition among individuals remain similar, we should have been able to detect a pattern.

Effects of brood size on nest defense.—We predicted that male and female flickers with larger broods should defend them more aggressively than flickers with smaller broods, but brood size was not correlated with any of the defense behaviors that we measured. Tryjanowski and Golawski (2004) suggested that brood size manipulation experiments are needed to adequately test for effects of brood size on nest defense. However, even some experimental studies have failed to reveal any differences in nest defense as a result of brood size (Tolonen and Korpimäki 1995). If parents optimize their clutch size according to their ability to raise all their young, then large and small broods may represent equal value to the defending adults, in which case brood size may not be expected to influence nest defense (Tolonen and Korpimäki 1995, Dawson and Bortolotti 2003).

In summary, anecdotal data from the literature (Lawrence 1967) and video-tape evidence from our own study site (KLW unpubl. data) indicates that the defense behaviors we observed may successfully protect cavity nests from live predators, such as red squirrels. Individual flickers varied in their re-

sponses, but we were unable to find strong correlates of that variation associated with common traits of those individuals or their broods.

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